

Rodents and climate II: Quantitative climatic estimates for Plio-Pleistocene faunas from Central Europe

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Abstract. A recently developed method for using arvicoline and murine rodents to estimate climatic parameters is applied to Plio-Pleistocene faunas from Central Europe. Mean annual temperature estimates using murines, which are highly diversified in the tropical regions of the Old World, are never lower than 11°C. On the other hand, the use of arvicolines, which occupied the temperate areas of the northern hemisphere, provides estimates ranging from -16.1°C for the coldest faunas to 16.9°C for the warmest faunas (similar to southern France today).

Key words: Rodents, climate, temperature, Central Europe, Pliocene, Pleistocene.

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I. INTRODUCTION

Many researchers are presently trying to establish a concordance between the evolution of species diversity and climate (e. g., HORÁČEK 1985, 1990; JANIS 1989; LEGENDRE 1987; LEGENDRE et al. 1991; MONTUIRE 1995). New approaches, using the species diversity of rodents, have recently been developed (AGUILAR et al. in press; MONTUIRE et al. in press) in order to quantify climatic parameters. These methods have here been applied to Pliocene and Pleistocene faunas from Hungary. Among the different climatic parameters, only temperature has been estimated in this study. In temperate areas such as Hungary, precipitation has not the same importance as in tropical or desert regions, and thus has not been considered here.

A c k n o w l e d g m e n t s. I wish to thank Serge LEGENDRE for his help in applying this new method of climatic parameter quantification to the Hungarian faunas. Bernard MARANDAT kindly helped me to translate the text into English. This is contribution no. 96-043 from the Institut des Sciences de l'Evolution, Montpellier (UMR 5554, CNRS).

II. METHODS

Among extant rodents, arvicolines and murines have a geographic distribution that is closely linked to the climate. The arvicolines have a Holarctic distribution and they are diversified in most northern areas, while being absent from the tropics. The murines, on the other hand, are confined

to the Old World. They are widespread in equatorial regions and absent in the coldest areas. Commensal species of murines, such as *Rattus rattus* and *Mus musculus*, are excluded from this study.

New methods have recently been developed to analyze this distributional relationship and estimate climatic parameters (MONTUIRE et al. in press). They are based on the relationship between these climatic parameters and species diversity as analyzed by simple linear regression. The number of species has been compiled for about 250 local faunas in the case of arvicolines and for 150 faunas in the case of murines. The associated climatic parameters have been taken from WERNSTEDT (1972). A local fauna covers an area of between 100 km² and 10 000 km².

It can be seen from Table I that the highest coefficient of determination (R^2) corresponds to the relationship between mean annual temperature and number of arvicoline species. This coefficient is greater than 0.8, which means that more than 80% of the variation in diversity can be explained by temperature variations. The coefficient of determination is also relatively high for the estimate of the mean temperature of the coldest month (R^2 near 0.75), while it is a little lower for the mean temperature of the warmest month (R^2 slightly under 0.6). Thus, the maximum temperature seems to place less constraint on diversity than the mean annual temperature and/or that of the coldest month.

The different coefficients of determination are lower for the murines (Table I). The relationship between arvicolines and temperature shows a negative slope (Table I), while that between murines and temperature is positive. Thus, these two relationships are each other's inverses.

Table I

Parameters of the least squares regression of temperature and number of species of Murinae and Arvicolinae (after AGUILAR et al. in press; MONTUIRE et al. in press). The climatic parameter estimated is the dependent variable: climatic parameter estimated = Number of species * Slope + Intercept. Abbreviations: Mur., Murinae; Arv., Arvicolinae; R^2 , coefficient of determination; Ann. temp., mean annual daily temperature; Min. temp., mean daily temperature of the coldest month; Max. temp., mean daily temperature of the warmest month

	R^2		Slope		Intercept		Error	
	Mur.	Arv.	Mur.	Arv.	Mur.	Arv.	Mur.	Arv.
Ann. temp.	0.49	0.83	1.15	-2.81	9.15	20.05	4.81	3.75
Min. temp.	0.52	0.77	1.77	-4.08	-1.03	12.88	7.11	6.49
Max. temp.	0.22	0.58	0.48	-1.56	19.34	27.22	3.80	3.88

III. MATERIAL

The method described above was applied to the 48 most complete fossil faunas in JÁNOSSY (1986). Among rodents, murines and arvicolines are generally well represented in European Plio-Pleistocene faunas. The definition of these subfamilies used here follows WILSON & REEDER (1993). In each fauna, all the species assigned to either murines or arvicolines have been taken into account.

The ages of the different faunas are given in Table II. In a few cases and notably for the youngest faunas, absolute ages are proposed by JÁNOSSY (1986). These have been obtained by radiocarbon dating. In other cases, the ages have been estimated from general indications. On the basis of several studies, JÁNOSSY (1986) also proposes a relative chronology of the different faunas. We have used this chronology to propose absolute ages for the faunas.

Table II

List of Hungarian faunas used in this study. Radiometric dates (*) were taken directly from JÁNOSSY (1986) or deduced from biostratigraphic indications found in that work. Number of species compiled from faunal lists after JÁNOSSY (1986)

Fauna	Age (ky)	Murinae	Arvicolinae
Baradla 4	5.0	3	6
Kis-Köhat	8.0	1	3
Rigó 5	9.1	2	4
Rigó 4	9.2	3	5
Rigó 3	9.3	3	5
Rigó 2	9.4	3	4
Rigó 1	9.5	4	4
Rejtek 1	12.0	3	8
Rejtek 9	13.0	2	7
Petényi Cave	15.0	3	8
Remetehegy 2	17.0	0	7
Remete Cave b	18.0	0	4
Remetehegy 1	19.0	0	5
Pilisszántó 3	20.0	0	8
Pilisszántó 2	23.0	0	5
Pilisszántó 1	25.0	0	8
Bivak Cave	28.7	0	3
Istállóskő Cave (*)	36.0	0	5
Tokod Nagyberek (*)	36.2	0	6
Erd (*)	40.0	1	5
Subalyuk 16-20 (*)	50.0	1	2
Kálmán V	70.0	1	4
Kálmán IV	75.0	1	5
Porlyuk	80.0	1	3
Süttő 9	90.0	2	6
Süttő 1-2-4	95.0	1	2
Hórvölgy	100.0	1	7
Castle Hill Hilton	200.0	1	4
Nagyharsányhegy 6	250.0	1	7
Uppony 3	263.0	1	9
Uppony 2	264.0	0	7
Uppony 1	265.0	1	10
25 Fortuna Street	290.0	2	4
Vértesszőlös 2	300.0	1	6
Tarkő 2	320.0	2	7
Tarkő 3	350.0	1	10
Tarkő 5-11	380.0	1	9
Kövesvárad	400.0	1	13
Somssich Hill 2	700.0	1	11
Osztramos 8	1100.0	1	6
Osztramos 2	1300.0	1	7
Nagyharsányhegy 4	1400.0	1	12
Villány 5	1800.0	3	11
Osztramos 3	2200.0	2	9
Villány 3	2300.0	2	8
Beremend 5	3100.0	1	3
Osztramos 7	3200.0	1	4
Csarnóta 2	4000.0	3	4

IV. RESULTS AND DISCUSSION

The climatic parameters estimated here are the mean annual temperature, the mean temperature of the coldest month and the mean temperature of the warmest month as a function of the number of arvicoline species. The results are presented, together with the error of the estimate and the prediction error, in Table III. In order to be read more easily, Figs. 1-3 have been separated into three time periods (4 000 Ka to 400 Ka, 400 Ka to 40 Ka, and 40 Ka to the Recent).

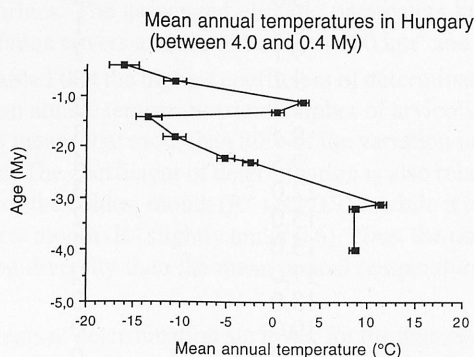


Fig. 1. Estimates of mean annual temperatures in Hungary between 4 Ma and 0.4 Ma. The curve shows the estimate together with its error.

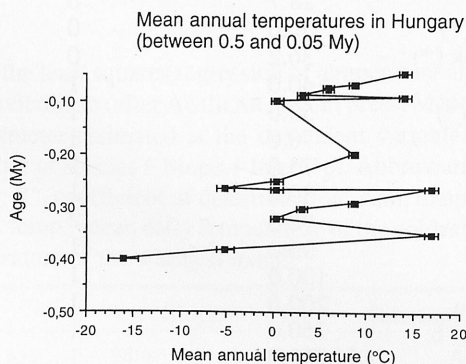


Fig. 2. Estimates of mean annual temperatures in Hungary between 0.4 Ma and 0.04 Ma. The curve shows the estimate together with its error.

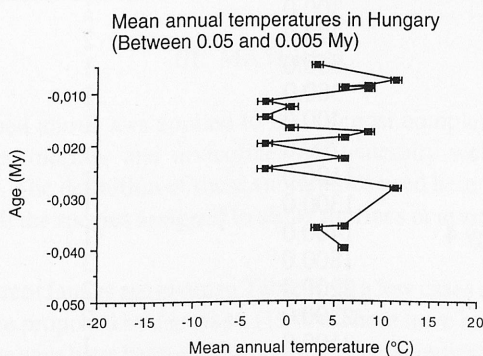


Fig. 3. Estimates of mean annual temperatures in Hungary between 0.05 Ma and the Recent. The curve shows the estimate together with its error.

Table III

Estimates of mean annual temperature, mean temperature of the coldest month, and mean temperature of the warmest month for the Hungarian faunas using arvicolines. The different temperature estimates are shown with the estimate (PE), the error of the estimate (EE) and the prediction error (EP)

Fauna	Ann. Temp.			Min. Temp.			Max. Temp.		
	PE	EE	EP	PE	EE	EP	PE	EE	EP
Baradla 4	3.1	0.29	3.97	-11.6	0.47	6.50	17.9	0.26	3.53
Kis-Köhat	11.4	0.27	3.97	0.7	0.44	6.50	22.7	0.24	3.53
Rigó 5	8.6	0.25	3.96	-3.4	0.41	6.49	21.1	0.22	3.53
Rigó 4	5.9	0.26	3.97	-7.5	0.42	6.49	19.5	0.23	3.53
Rigó 3	5.9	0.26	3.97	-7.5	0.42	6.49	19.5	0.23	3.53
Rigó 2	8.6	0.25	3.96	-3.4	0.41	6.49	21.1	0.22	3.53
Rigó 1	8.6	0.25	3.96	-3.4	0.41	6.49	21.1	0.22	3.53
Rejtekt 1	-2.4	0.40	3.98	-19.9	0.66	6.51	14.7	0.36	3.54
Rejtekt 9	0.4	0.34	3.97	-15.8	0.56	6.50	16.3	0.30	3.53
Petényi Cave	-2.4	0.40	3.98	-19.9	0.66	6.51	14.7	0.36	3.54
Remetehegy 2	0.4	0.34	3.97	-15.8	0.56	6.50	16.3	0.30	3.53
Remete Cave b	8.6	0.25	3.96	-3.4	0.41	6.49	21.1	0.22	3.53
Remetehegy 1	5.9	0.26	3.97	-7.5	0.42	6.49	19.5	0.23	3.53
Pilisszántó 3	-2.4	0.40	3.98	-19.9	0.66	6.51	14.7	0.36	3.54
Pilisszántó 2	5.9	0.26	3.97	-7.5	0.42	6.49	19.5	0.23	3.53
Pilisszántó 1	-2.4	0.40	3.98	-19.9	0.66	6.51	14.7	0.36	3.54
Bivak Cave	11.4	0.27	3.97	0.7	0.44	6.50	22.7	0.24	3.53
Istállóskő Cave	5.9	0.26	3.97	-7.5	0.42	6.49	19.5	0.23	3.53
Tokod Nagyb.	3.1	0.29	3.97	-11.6	0.47	6.50	17.9	0.26	3.53
Erd	5.9	0.26	3.97	-7.5	0.42	6.49	19.5	0.23	3.53
Subalyuk 16-20	14.1	0.31	3.97	4.9	0.51	6.50	24.3	0.28	3.53
Kálmán V	8.6	0.25	3.96	-3.4	0.41	6.49	21.1	0.22	3.53
Kálmán IV	5.9	0.26	3.97	-7.5	0.42	6.49	19.5	0.23	3.53
Porlyuk	5.9	0.26	3.97	-7.5	0.42	6.49	19.5	0.23	3.53
Süttő 9	3.1	0.29	3.97	-11.6	0.47	6.50	17.9	0.26	3.53
Süttő 1-2-4	14.1	0.31	3.97	4.9	0.51	6.50	24.3	0.28	3.53
Hórvölgy	0.4	0.34	3.97	-15.8	0.56	6.50	16.3	0.30	3.53
Castle Hill	8.6	0.25	3.96	-3.4	0.41	6.49	21.1	0.22	3.53
Nagy. 6	0.4	0.34	3.97	-15.8	0.56	6.50	16.3	0.30	3.53
Uppony 3	-5.1	0.47	3.99	-24.0	0.77	6.53	13.1	0.42	3.54
Uppony 2	0.4	0.34	3.97	-15.8	0.56	6.50	16.3	0.30	3.53
Uppony 1	16.9	0.37	3.97	9.0	0.61	6.51	25.9	0.33	3.53
25 Fortuna Str.	8.6	0.25	3.96	-3.4	0.41	6.49	21.1	0.22	3.53
Vértesszőlös 2	3.1	0.29	3.97	-11.6	0.47	6.50	17.9	0.26	3.53
Tarkő 2	0.4	0.34	3.97	-15.8	0.56	6.50	16.3	0.30	3.53
Tarkő 3	16.9	0.37	3.97	9.0	0.61	6.51	25.9	0.33	3.53
Tarkő 5-11	-5.1	0.47	3.99	-24.0	0.77	6.53	13.1	0.42	3.54
Kövesvárad	-16.1	0.78	4.03	-40.5	1.28	6.61	6.6	0.69	3.59
Somssich Hill 2	-10.6	0.62	4.01	-32.3	1.02	6.56	9.8	0.55	3.56
Osztramos 8	3.1	0.29	3.97	-11.6	0.47	6.50	17.9	0.26	3.53
Osztramos 2	0.4	0.34	3.97	-15.8	0.56	6.50	16.3	0.30	3.53
Nagy. 4	-13.4	0.70	4.02	-36.4	1.15	6.58	8.2	0.62	3.57
Villány 5	-10.6	0.62	4.01	-32.3	1.02	6.56	9.8	0.55	3.56
Osztramos 3	-5.1	0.47	3.99	-24.0	0.77	6.53	13.1	0.42	3.54
Villány 3	-2.4	0.40	3.98	-19.9	0.66	6.51	14.7	0.36	3.54
Beremend 5	11.4	0.27	3.97	0.7	0.44	6.50	22.7	0.24	3.53
Osztramos 7	8.6	0.25	3.96	-3.4	0.41	6.49	21.1	0.22	3.53
Csarnóta 2	8.6	0.25	3.96	-3.4	0.41	6.49	21.1	0.22	3.53

As the temperatures obtained using data on murines do not vary significantly, they have not been taken into account in the different figures. Murines are widely distributed over the tropical areas of the Old World (MISONNE 1969) and provide mean temperature estimates of around 11°C. Despite a relatively good coefficient of determination, murines show the limits of application of this model in temperate areas.

The arvicolines, which occupy the temperate areas of the Northern Hemisphere provide indications of more important changes in the climatic parameters (Figs. 1-3). As estimated, the mean annual temperatures range from -16.1°C for the coldest faunas to 16.9°C for the warmest ones (Table III). The mean temperature estimates for the coldest month range from -40°C to 9°C and those for the warmest month from 6.6°C to 25.9°C (Table III).

Temperature minima occur at 1.4 Ma and 400 000 Ka. Other important drops in temperature occur at 2.3 and 1.8 Ma, and 700 000, 270 000 and 100 000 Ka. Periods of increasing temperature seem less important.

In another study, also based on Hungarian faunas (MONTUIRE 1995), it is shown that variations in species diversity are related to climatic changes seen in isotopic curves (IMBRIE et al. 1984; SHACKLETON & HALL 1985). Decreases in species diversity have been related to important decreases in temperature at different periods: 2.3 Ma, 400 000, 300 000, 100 000 and 50 000 Ka (MONTUIRE 1995). These decreases are also found in this study, but temperature minima dated to 1.8, 1.4 and 0.7 Ma are seen for the first time. There is an increase in temperature between 12 000 and 9 500 Ka. A maximum in species diversity, coincident with an increase in ocean temperatures and the beginning of the Quaternary deglaciation has been dated to approximately 15 000 Ka. The difference observed between these dates may be artifactual: the isotopic events are much more securely dated than the Hungarian micromammal faunas used here.

The method of quantifying climatic parameters has brought to light new information on the climatic events in the area under study. Despite the differences between the two approaches, on one hand specific diversity analysis, and on the other hand climatic parameters quantification, similar results are obtained, which confirms the relationship between changes in species diversity and changes in climate.

It can sometimes be difficult to correlate a diversity event with a specific climatic event. Besides problems of systematics, the main difficulty lies in the calibration of the faunas, which may have a smoothing effect on the results. The available record being discontinuous, what is shown are only trends in the temperature record. A greater number of better dated faunas will be necessary to refine these correlations. Comparisons between the results obtained using the two approaches should bring to light additional information on the correlations obtained with climatic events as recorded on the isotopic curves and consequently more accurate dating of the faunas.

V. CONCLUSIONS

The method outlined in this paper allows quantification of some climatic parameters, leading to a demonstration of the major changes in temperature that have occurred during the Quaternary. The murines show the limits of application of this method in temperate areas, and the arvicolines have instead been used, since the analysis is confined to the Palaearctic. The temperature estimates range from -16.1°C to 16.9°C for mean annual temperature, -40.5°C to 9.0°C for mean temperature of the coldest month and, 6.6°C to 25.9°C for mean temperature of the warmest month.

The method has in this study been used for Hungary, but can be applied to other Eurasian regions as well. Thus, we can expect to show differences within Europe or Eurasia between eastern and western regions, i. e., between continental and oceanic influence on the climate, or between south and north, i. e., between temperate and mediterranean climates. In the same way, the

arvicolines that are used to estimate the climatic parameters will allow us to compare Europe and North America, because this subfamily is widely distributed across these two continents.

We can also compare the results obtained with this method with other quantification methods, for example the results of malacological (e. g., ROUSSEAU 1991) and palynological (e. g., GUIOT 1990) studies.

We see in this present work that we can use rodents to estimate climatic parameters, and in the specific case of the geographical area studied we selected data on arvicolines. It is also possible to use other families, such as murines. It will be interesting in the future to extend and apply the methods to other groups, such as ungulates and marsupials.

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